FUSION OF FILAMENTS IN THE LAMELLIBRANCH GILL.

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It is far from the purpose of this paper to enter fully into the discussion of the morphology of the lamellibranch gill; but a brief preliminary statement of a general nature may serve to define the terminology employed, and to simplify the following more detailed description of a single point in the gill structure.

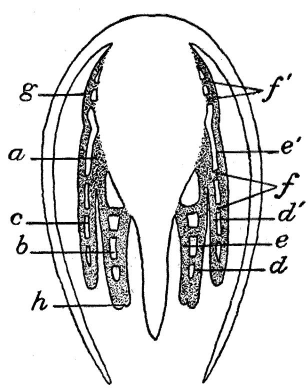


FIG. 1. — Diagrammatic frontal section of lamellibranch. Shell omitted; gills shaded. *a*, gill axis; *b*, inner gill; *c*, outer gill; *d* and *d'*, descending lamellae of inner and outer gills; *e* and *e'*, ascending lamellae of inner and outer gills; *f* and *f'*, interlamellar connections of gill and dorsal appendage; g, dorsal appendage of outer gill.

When the animal is oriented in the usual manner, with the hinge line upward, the gills hang down on either side, between the body and mantle, as shown in Fig. 1. Strictly considered, there is but one gill, or one ctenidium, on each side of the body. This ctenidium consists, fundamentally, of a slight longitudinal ridge along the side of the body, the gill axis (Fig. 1, *a*), and a double row of ciliated filaments, which extend downward into the mantle cavity of the animal and are then reflected upward. In common language each of these rows of filaments, or the structure arising therefrom, is termed a gill; and I shall retain this convenient, though morphologically indefensible term, and designate that half of the ctenidium next the body as the inner gill (Fig. 1, *b*), and that half next the mantle as the outer gill (Fig. 1, *c*).

In some few forms the adjacent gill filaments remain entirely free from one another, *e.g.*, Anomia; in other forms, as Mytilus and Pecten, there is a union by means of tufts of very long interlocking cilia — ciliated discs. In contrast to these two types,

which may be grouped together as filamentous gills, we find in the great majority of lamellibranchs a more or less strong development of vascular connections between the filaments, binding them together to form the lamellae from which the class takes its name. Such gills may be termed lamellar.

As each filament consists of two limbs, a descending and an ascending, so each gill is composed of two lamellae, correspondingly designated as descending (Fig. 1, *d* and *d'*) and ascending (Fig. 1, *e* and *e'*). These lamellae are usually connected with one another by more or less complicated interlamellar connections (Fig. 1, *f*).

The ascending lamella of the inner gill may remain free, or its upper margin may fuse with the body and, behind the body, with the corresponding part of the gill of the other side. The ascending lamella of the outer gill may lie free in the mantle cavity or may be attached to the mantle on a level with the gill axis; or it may be continued dorsally above this line, forming a dorsal appendage (Fig. 1, *g*), which is finally attached to the body, or rather to the fusion line of mantle and body. Thus the dorsal appendage consists of the ascending lamella alone, and may show a structure decidedly different from that of the gill proper. Connections similar to the interlamellar connections of the gill attach the dorsal appendage to the body wall (Fig. 1, *f'*).

The lower free margin of some gills is smoothly rounded off; in other cases the border is deeply notched by a groove running from end to end of the gill. This may be called the marginal groove. In the diagram the groove is seen in cross-section in the inner gill (Fig. 1, *h*), while the outer gill presents a smooth margin with no sign of a furrow. Exactly these conditions are found in a large number of lamellibranchs, *e.g.*, Astarte, Dreissensia, Cardium, Psammobia. It may be suggested in passing that the somewhat unintelligible distinction of "double gills" and "single gills," in the classical paper by Williams,[1] may perhaps be based on the presence or absence of this marginal groove.

[1] Williams, T., "Respiratory Organs of Invertebrates," *Annals and Magazine of Natural History*. Vol. xiv. 1854.

The surface of the gill lamellae may show either of two types. It may be smooth, all the filaments lying in one plane; or, with the requirement of greater respiratory surface, the lamellae may be folded parallel to the filaments. The two lamellae of one gill are always folded symmetrically, so that the section of the gill perpendicular to the filaments assumes an outline reminding one, in its extreme form, of a string of wooden button molds. Both filamentous and lamellar gills are subject to this folding.

The filaments occupying the bottom of the reëntrant folds, the limiting filaments, are usually somewhat larger than the intermediate filaments, and are often very much modified in form as well as size. These filaments may be easily traced through the whole height of the gill and afford a series of fixed points, aiding materially in the study of the folded type of gill by means of sections.

From the above résumé it is evident that fusion or concrescence of parts has long been recognized in the lamellibranch gill. Even in simple filamentous gills (Mytilus, etc.) the tips of the filaments fuse to form a continuous band along the margin of the ascending lamella. In more complex forms it is a process of fusion which transforms the rows of originally distinct filaments into the characteristic lamellae. The fusion of the ascending lamellae with the mantle and body is also perfectly familiar. But the particular type of fusion described below appears to have escaped mention in the somewhat extensive literature upon the lamellibranch gill.

Even a hasty study of serial sections of the strongly folded gill of *Cardium edule* or *Batissa tenebrosa* shows the somewhat surprising fact that each fold contains a far larger number of filaments in the upper portion of the gill than in the neighborhood of the free margin, this being equally true of ascending and descending lamellae. (The extreme case was noted in Cardium, where the number of filaments in one fold increased from eight to thirty.) Yet the limiting filaments are continuous throughout, showing that there is no reduction in the number of folds correlated with the increase in the number of filaments in each fold. These observations appear at first sight irreconcilable with

the theory of gill development advanced by Lacaze-Duthiers[1] and universally accepted, according to which the ascending limbs of the filaments are essentially the reflected tips of the originally simple straight filaments. The larger number of filaments in the upper parts of the descending lamellae could be explained by the assumption of the presence of a large number of abortive filaments. But this explanation, unsatisfactory even for the descending lamellae, cannot apply to the ascending lamellae.

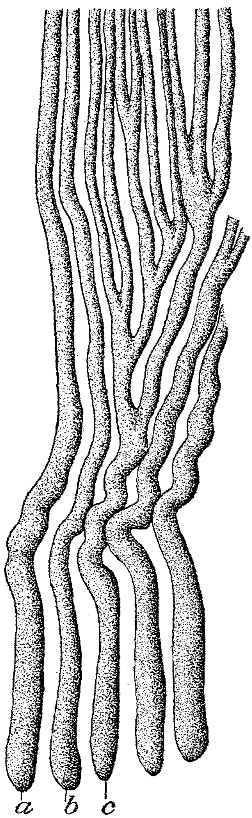


FIG. 2. — Surface view of group of filaments of inner gill of *Batissa tenebrosa*. × 60. Lower edge of figure represents the free margin of gill. Cilia and complex interfilamentary connections omitted for the sake of clearness. *a* and *b*, simple filaments; *c*, compound filament, formed by fusion of nine simple filaments.

A more detailed study of serial sections, and, better, of microscopic dissections in which the lamellae are separated and the folds spread out as smooth as possible, shows clearly that the filaments of the upper portion gradually meet and fuse as the free margin of the gill is approached. This phenomenon is illustrated by Figs. 2 and 3. In the former we have a surface view of a small portion of the inner gill of *Batissa tenebrosa*, extending upward from the free edge. While the two filaments at the left (Fig. 2, *a* and *b*) are simple throughout, the next filament (Fig. 2, *c*), indistinguishable from the others at its lower end, is really formed by the fusion of nine filaments.

In this species such groups of fusing filaments are found principally in the projecting folds of the gill, very seldom in the reëntrant folds. In *Cardium edule*, on the other hand, the fusion is more marked in the reëntrant than in the projecting folds.

[1] Lacaze-Duthiers, H. de, "Mémoir sur le développement des branchies des Mollusques Acéphales Lamellibranches," *Annales des Sciences Naturelles*. Zoologie Sér. iv, Tome v. 1856.

Fig. 3 represents diagrammatically the surface of a single fold of this species, each filament being represented by a simple line. At the gill margin (lower side of diagram) there are eight filaments, including the limiting filaments (Fig. 3, *a* and *h*); in the upper part of the gill (and diagram) there are thirty. Of these thirty filaments, twenty-one unite to form the two limiting filaments (Fig. 3, *a* and *h*) and the two adjacent intermediate filaments (Fig. 3, *b* and *g*), which occupy the reentrant folds. The remaining four intermediate filaments (Fig. 3, *c*, *d*, *e*, and *f*), those of the projecting fold, are formed by the union of only nine filaments. The irregularity of the fusion is also well shown by this diagram. Note especially that one limiting filament is entirely simple, while the other is the resultant of the fusion of seven simple filaments.

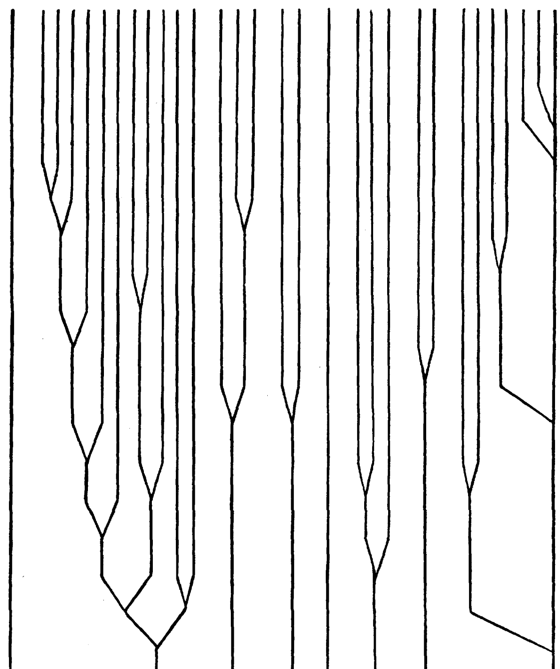


Fig. 3. — Diagrammatic view of surface of fold of inner gill of *Cardium edule*, illustrating fusion of filaments. Filaments represented by lines. Lower edge of diagram represents free margin of gill. *a* and *h*, limiting filaments; *b–g*, intermediate filaments.

The fusion is usually almost exclusively limited to a somewhat narrow zone in the near vicinity of the free margin of the gill. In this zone may also be noted a gradual reduction in the folding of the gill as the margin is neared. In those lamellibranchs whose outer gill is provided with a dorsal appendage, there is a second zone of fusion along the transition line from

the gill proper to the appendage. This line again marks a partial or total obliteration of the folding of the gill — a point of importance in the consideration of the meaning and cause of the fusion of the filaments.

The term "fusion of filaments" has been employed repeatedly; but the question arises whether the phenomenon under discussion is really a fusion of a large number of once distinct filaments or a branching of a relatively small number of original filaments; whether, in other words, the primary filaments are represented by the maximum or minimum number. The answer is not far to seek. At the free margin of the gill the continuity of the filaments may be readily traced from one lamella to the other, and the number of filaments in the two lamellae within any given fold must necessarily be equal. A little higher, in the zone of fusion, these numbers may become very unequal. For example, in a section of the gill of Batissa seven filaments of one lamella were observed to correspond to twelve in the other. Neither of these facts, however, offers conclusive evidence; both may be explained as well on the supposition of branching as on that of fusion. But as the serial sections are followed a little higher in the gill, the inequality in the number of filaments, which has increased from zero at the margin to a maximum in the zone of fusion, begins to fall off again more or less rapidly, and finally reduces itself once more to zero. This equality in the number of filaments in the upper parts of the gill can be explained only on the supposition that the phenomenon before us is a fusion, not a branching, of the gill filaments. It is altogether too improbable that the independent branching of the filaments in the two lamellae would lead to the same number in the two cases.

Granted that the phenomenon is a fusion, what is its meaning? Is it of systematic importance? My observations are not complete enough to permit a categoric answer; but I am strongly inclined to the belief that the fusion carries no more of weight from the systematic standpoint than does the folding of the gill.

Among smooth gills no fusion was observed, although a considerable number of forms were studied. Especial attention was devoted to Tellina and Scrobicularia, in which, for reasons

detailed in an earlier paper,[1] I consider the simplicity and smooth surface of the gill to be secondary characters — a retrograde development from the folded gill type of the Veneridae. Fusion was also never observed in the filamentous type of gill.

The results of my own observations upon the folded lamellar gills may be tabulated as follows:

1. Fusion strongly developed: *Cardium edule* Lin., *Chama pellucida* Brod., *Batissa tenebrosa* Hinds, *Psammobia vespertina* Lin., *Donax serra* Chemn.

2. Fusion moderately developed: *Venus verrucosa* Lin., *Cyprina islandica* Lin., in latter strongly developed on transition line from outer gill to appendage.

3. Fusion very slightly developed: *Eusatella americana* Verrill, *Mya arenaria* Lin., *Donax politus* Poli, in latter perhaps accidental.

4. No fusion observed: *Cytherea chione* Lin., *Donax trunculus* Lin., *Ostrea virginiana* Lister, *Thracia papyracea* Poli.

Lima and Ostrea should probably be added to the list of forms in which fusion occurs, though on somewhat doubtful evidence, which will be mentioned later.

Thus we find this fusion of filaments similarly developed in widely separated forms, belonging to very diverse groups; on the other hand, within the single genus Donax we find all grades of fusion, as we also find all grades of folding.

This parallelism of folding and fusion in the genus Donax appears to me to furnish, in a certain sense, an epitome of the whole matter, for I consider the fusion of the filaments to be a mechanical correlative of the folding of the lamellae. The process may be pictured in something this way. The folding of the lamellae is gradually developed in the young lamellibranch as the increasing number of filaments becomes too great to lie in one plane. But at the free margin the filaments are bound somewhat firmly together and the folding is somewhat reduced. This leads to a crowding together of the filaments at this point and eventually to an organic fusion of the same. How great the crowding must really be in the strongly folded forms may be inferred from the fact that the upper part of the inner gill of

[1] "Die systematische Verwertbarkeit der Kiemen bei den Lamellibranchiaten," *Jenaische Zeitschrift für Naturwissenschaft.* Bd. xxxi. 1897.

Cardium edule would measure, if flattened out, fully seven times the length of the free margin of the same gill. The absence of fusion in filamentous gills, even where the folding is extreme, as in Pecten, may be easily explained on the ground of the looser structure of the gill and the possibility of a displacement of the filaments, with consequent relief of pressure.

It is an interesting point in this connection that no fusion was observed in the outer gill of either Psammobia or Cardium, although it is conspicuous in the inner gill. In both cases the inner gill is provided with a deep marginal groove, while the outer gill shows no sign of this structure. The presence of this marginal groove is the mechanical equivalent of a shortening (slight to be sure) of the margin of the gill, the bottom of this groove being almost perfectly straight, and therefore slightly shorter than the somewhat scalloped margin of the folded gills in which no groove is present. Hence we find in this characteristic a cause of increased crowding and increased fusion.

For a very short distance above each point of fusion one observes a slight modification of the epithelium of those sides of the fusing filaments which are turned toward each other. The nuclei are somewhat larger and more closely crowded, as shown diagrammatically in Fig. 5. Aside from this, no histological distinction can be drawn between the simple original filaments of the upper portion of the gill and the compound filaments of the lower margin. Even in the matter of size there is no noticeable difference except in the immediate vicinity of the fusion, where the compound filament is considerably enlarged. This statement is made after comparison of a large number of preparations, and seems to be the rule, although there are considerable individual variations in different specimens. The apparent larger size of the compound filaments in Fig. 2 is to be explained in part on the ground of such individual variations. It is due in larger degree, however, to slight differences in the position of the filaments, which are elliptical in cross-section, and appear of different size according as one or another side is presented to view. It should also be noted that the filaments are somewhat enlarged at the extreme margin of the gill, and that these enlarged tips are shown in the figure.

As regards the size and finer structure of the filaments, the evidence of sections is more reliable than that of surface preparations; and in Figs. 4–8 are represented a series of sections through a group of filaments of the inner gill of *Cardium edule*. The same filaments are shown in all the figures, although the very complex interfilamentary and interlamellar connections, differently cut in the different sections, cause a considerable variety of aspect. These connections may be disregarded in the present discussion. In Fig. 4, which represents the uppermost section, six filaments are shown, all practically alike. In

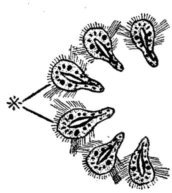


FIG. 4.

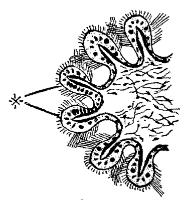


FIG. 5

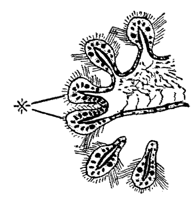
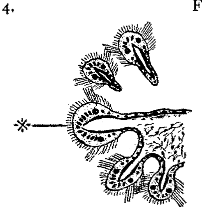


FIG. 6.



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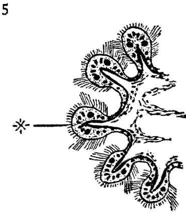

FIG. 8.

FIGS. 4–8. — Series of sections through group of filaments of inner gill of *Cardium edule*. × 95. Cilia and nuclei somewhat diagrammatic. Fig. 4 is uppermost section. Asterisk marks two simple filaments fusing to one compound.

Fig. 5 two of these, marked with an asterisk in all the figures, show a slight modification of the epithelium, as described above. This section is immediately above the point of fusion of the two filaments. Fig. 6 shows these filaments so closely approximated that they may almost be described as forming a single deeply grooved filament, a condition better shown by other preparations. In Fig. 7 the fusion is complete, but the compound filament is still considerably enlarged; while in Fig. 8 the compound filament has regained its normal size and form, and the transition is complete.

Strangely, this very conspicuous fusion of the filaments appears to have received little or no notice. I have been able to find no reference whatever in the text of any articles at my

disposal. Only in the figures is a possible hint of its observation. Thus in the exquisite work by Deshayes[1] on the Mollusca of Algiers there is a small figure of the gill of Pholas, in which two incomplete filaments are interpolated among those which extend through the whole height of the gill. In the one the free end is turned upward; in the other, downward. Do these represent two filaments fusing with their neighbors? If so, the difference in direction in the two cases clearly distinguishes the phenomenon from that described above. Moreover, the author's description of the gill as entirely smooth makes a fusion *a priori* improbable. An inaccuracy in the drawing, which is very small, is the simpler explanation.

In a considerable number of more recent figures a single fold of the gill is represented in section as containing an unequal number of filaments in the two lamellae, thus in Cardium (van Haren),[2] Lima (Pelseneer),[3] *Donax trunculus* (Sluiter),[4] and Ostrea (Kellogg).[5] It will be noted that in the last two cases the figures cited do not accord with my own observations. But my purely negative verdict of "not observed" contains no direct contradiction of the affirmative statements of these authors. While I am convinced that my own preparations show no evidence of a fusion of filaments in Ostrea and *Donax trunculus*, I consider it probable that the figures of Kellogg and Sluiter, as well as those of van Haren and Pelseneer, point to a greater or less development of the phenomenon described. Unfortunately no certain conclusions can be reached in the absence of corroboration in the accompanying text.

[1] Deshayes, G. P., "Exploration scientifique de l'Algérie," *Zoologie*. Tome i, No. 4. Paris, 1849.

[2] Haren-Noman, D. van, "Die Lamellibranchiaten, gesammelt während der Fahrten des Willem Barents, 1878 and 1879," *Niederländisches Archiv für Zoologie*. Supplementband I, 1881–82.

[3] Pelseneer, P., "Contribution à l'étude des Lamellibranches," *Archives de Biologie*. Tome xi. 1891.

[4] Sluiter, C. P., "Beiträge zur Kenntniss des Baues der Keimen bei den Lamellibranchiaten," *Niederländisches Archiv für Zoologie*. Bd. iv. 1878.

[5] Kellogg, J. L., "A Contribution to our Knowledge of the Morphology of the Lamellibranchiate Mollusks," *Bulletin of the U. S. Fish Commission*. Vol. x. 1890.

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